

# Behavioural syndromes in Merriam's kangaroo rats (*Dipodomys merriami*): a test of competing hypotheses

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Behavioural syndromes, correlations of behaviours conceptually analogous to personalities, have been a topic of recent attention due to their potential to explain trade-offs in behavioural responses, apparently maladaptive behaviour and limits to plasticity. Using Merriam's kangaroo rats (*Dipodomys merriami*), we assessed the explanatory power and generality of hypothesized syndrome structures derived from the literature and the natural history of the species. Several aspects of functionally distinct behavioural responses of *D. merriami* were quantified. Syndrome structures were compared using structural equation modelling and model selection procedures. A domain-general behavioural syndrome incorporating cross-functional relationships between measures of boldness, agonistic behaviour, flexibility and food hoarding best explained the data. This pattern suggests that *D. merriami* behaviours should not be viewed as discrete elements but as components of a multivariate landscape. Our results support arguments that a lack of independence between behaviours may be a general aspect of behavioural phenotypes and suggest that the ability of *D. merriami*'s behaviour to respond to selection may be constrained by underlying connections.

**Keywords:** behavioural syndromes; personality; *Dipodomys merriami*; structural equation modelling; shy–bold

## 1. INTRODUCTION

The role of individual variation in ecology and evolution has sometimes been neglected as a simplifying assumption for both statistical analyses and development of general theories about behaviour. However, such an assumption ignores the role of individual variation in natural selection (Darwin 1859; 1998) and widespread theoretical and observational support for the maintenance of polymorphisms in populations (Smith & Skulason 1996; Bergstrom & Godfrey-Smith 1998; Doebeli *et al.* 2007). Departing from the view of individuals as statistical noise allows increased attention to be paid to the importance of individual variation in all areas of ecological and evolutionary research (Hayes & Jenkins 1997; Bolnick *et al.* 2003) and has revealed the presence of behavioural syndromes in individuals (Sih *et al.* 2004b; Bell 2005, 2007).

Behavioural syndromes, conceptually analogous to personalities, are the consistent coupling of behavioural responses and range in complexity from cross-functional correlations of as few as two behaviours (e.g. anti-predator behaviour correlated with conspecific aggression; Sih *et al.* 2003) to complex personality structures based on factor analysis (Gosling & John 1999). Syndrome or personality differences between individuals are well recognized in humans and have been identified in a wide variety of other animals (Mather & Anderson 1993; Gosling 1998; Dingemanse *et al.* 2004; Bell 2005; Stapley & Keogh 2005). These individually consistent responses have been found to be heritable (Koolhaas *et al.* 1999; Dingemanse *et al.* 2002) and may impact fitness (Buss & Greiling 1999; Dingemanse *et al.* 2004; Dingemanse & Reale 2005).

Syndrome characteristics may be highly variable between species and environments and have important ecological and evolutionary implications due to the inherent trade-offs of a syndrome structure (Sih *et al.* 2004a). These trade-offs result from correlations between behaviours, implying that selective pressures cannot operate on single behavioural responses independently (Lande & Arnold 1983). Depending on the nature of the correlation, one or more behavioural responses may be prevented from reaching local optima in order for the suite of behaviours to reach a multivariate maximum (Roff & Fairbairn 2007). Further, behavioural syndromes that constrict plasticity and response options for individuals may represent frequency- or density-dependent effects or be alternative strategies maintained by multiple optima (Price & Langen 1992; Sinervo & Lively 1996).

Since behavioural syndrome structures have been described in multiple species, we can now ask whether previously described structures are present across taxa. This will eventually allow the use of phylogenetic methods to more properly determine the ecological, developmental and phylogenetic determinants of behavioural syndromes.

To determine the generality of syndrome structures, we tested hypothesized syndrome structures in Merriam's kangaroo rats (*Dipodomys merriami*). Kangaroo rats are appropriate species for syndrome research because they exhibit extensive intraspecific behavioural variation (e.g. alternative food caching behaviours and mating strategies; Jenkins *et al.* 1995; Randall *et al.* 2002; Murray *et al.* 2006), and the wide distribution of some species, including *D. merriami*, may necessitate diverse coping strategies within and between populations to deal with variation in local conditions.

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We quantified behavioural responses from three functional contexts in *D. merriami*. First, we measured a proxy for status in agonistic interactions and intraspecific aggression. Agonistic behaviour towards conspecifics is often a defining characteristic of behavioural syndromes and may help in defining the trade-offs of complex syndromes (Sih *et al.* 2004b). Second, we quantified the seed caching behaviour of individuals. *D. merriami* stores seeds in scatter hoards (numerous dispersed caches) or larder hoards (one location, typically a burrow; Jenkins *et al.* 1995). Caching behaviour affects survival because individual *D. merriami* store food for later use during periods of low availability, exhibiting a range of expression between complete larder hoarding and complete scatter hoarding (Jenkins *et al.* 1995). We also quantified the intra-individual flexibility exhibited in caching behaviour (Asendorpf 1990). Finally, we quantified the foraging behaviour in the presence of a predator stimulus as a measure of boldness, a frequent component of syndromes (Sih *et al.* 2004a,b).

We tested hypothesized structures of behavioural syndromes containing responses from the above behaviours. These included syndromes analogous to the shy–bold continuum (Wilson *et al.* 1994), alternatives (Sih *et al.* 2004b) and an unstructured null model of behavioural independence. Syndrome structures were compared using structural equation modelling (SEM) and AIC-based model comparison (Burnham & Anderson 2002; Johnson 2002; Shipley 1999). This combination of SEM and model comparison allowed the first explicit testing of multiple proposed models of syndromes in behavioural ecology.

## 2. MATERIAL AND METHODS

Nineteen adult male *D. merriami* were obtained from locations 70 km east of Reno, Nevada and housed and tested in the animal care facility of the Department of Biology, University of Nevada, Reno. Only adult male *D. merriami* were used to avoid the possibility of conflating individual differences with sex or age differences. Animals were individually housed with a 12 : 12 light : dark cycle and fed ad libitum quantities of bird seed except during limited fasting periods (see §2a(ii)). Trapping was conducted over a one-month period and behavioural trials commenced two months after all individuals were collected and brought into the laboratory. All behavioural testing occurred during dark time periods.

### (a) Behavioural tests

#### (i) Agonistic behaviour

We quantified status in agonistic interactions as represented by response to mirror-image stimulation (MIS; Svendsen & Armitage 1973). MIS response is strongly related to agonistic behaviour during staged pairwise encounters of *D. merriami* (Hargett 2006) and has been used to assess behavioural syndromes in other species (Armitage & Van Vuren 2003; Blumstein *et al.* 2006). In addition, MIS standardizes the stimulus to which a subject responds to an image of equal size; thus, measures of aggression are not confounded by size differences between the focal subject and a conspecific.

We conducted MIS testing in 1.2 × 1.2 m arenas with a small dish containing 10 g of millet seed along a wall of the arena that also had a covered mirrored surface extending

11.7 cm in height and 1.2 m in length. A rock and branch were located in the half of the arena farthest from the mirrored wall. These objects provided visual refuge from reflections. We released a subject into the back-right (relative to the mirror) quadrant of the arena and allowed it to explore the arena for 10 min. At the end of this acclimation period, the curtain was removed from over the mirror and we continuously recorded the subject's behaviour for 15 min (Martin & Bateson 1999). For the purpose of comparing the models of syndrome structure, we used the time taken by an individual to resume activity after viewing its reflection as a response variable (latency). Latency is negatively correlated with aggression levels and dominance status (Hargett 2006) and we considered it a measure of aggressiveness and response towards conspecifics. Individuals with lower latency times were more likely to attack their mirror image and were more active in the half of the arena containing the mirror. Conversely, individuals with higher latency times froze or fled from their reflections. Elsewhere (Hargett 2006), *D. merriami* with lower latency times were also found to be more aggressive towards conspecifics and vice versa.

#### (ii) Variation in caching strategy

Individual variation in caching behaviour was determined by quantifying patterns of seed caching in 1.45 m<sup>2</sup> arenas. Caching behaviour was observed in the presence of differing cues of conspecific presence. Arenas were filled to a depth of 2.5 cm with fine sand and had a mesh screen on top of a removable wooden floor (Jenkins *et al.* 1995). Artificial burrows built of opaque PVC pipe were provided to individuals during caching trials.

Subjects were placed in arenas and provided with 20 g of millet seed in a small dish after a 10-h fasting period. After one complete dark cycle, the individual was removed and the locations and masses of seed caches recorded. This procedure was repeated for four trials per subject with each trial differing by cue of conspecific presence (see below). Each trial was separated by one week.

Four different cues of conspecific presence were used during trials to determine the differences in caching behaviour under different levels of perceived pilferage risk. First, we assessed caching behaviour in the presence of conspecific olfactory cues. An area surrounding the seed dish of approximately 625 cm<sup>2</sup> contained sand in which conspecifics had scent marked. Second, we assessed caching behaviour in the presence of conspecific visual cues by recording caching behaviour when one wall of the arena had a mirror extending 1.2 m along its length and 11.7 cm vertically. This mirror simulated the presence of a conspecific (Svendsen & Armitage 1973 and above). The seed dish was placed along the middle of the mirrored wall. Third, we assessed caching behaviour in the presence of both visual and olfactory cues by combining the above two treatments. Finally, we assessed caching behaviour in the absence of visual and olfactory cues. Testing order was determined by random assignment of individuals to a testing sequence generated by a 4 × 4 Williams square (Diaz-Uriarte 2002). We will describe differential responses to different conspecific cues in greater detail in subsequent publications.

We used a simulation model to compute a spatial index of the dispersion of caches in scatter hoards and the larder hoard as an estimate of vulnerability of caches to pilferage. The spatial index was the minimum time required for complete exploitation of food caches by a simulated naive forager searching, using area

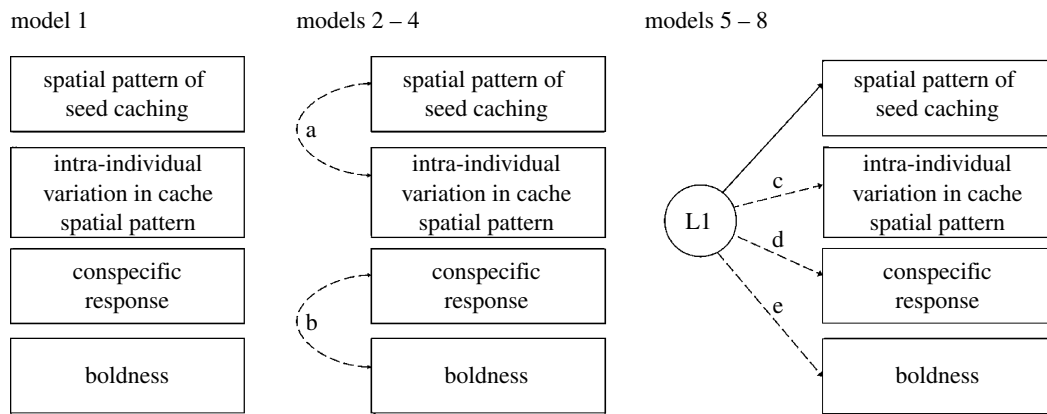


Figure 1. Models (1–8) of hypothesized relationships between behaviours, i.e. syndrome structures. Models are described in the text. Model comparison results are given in table 2. Unidirectional arrows represent causal relationships between a latent variable (L1) and behavioural responses. Bidirectional arrows represent an undefined correlation between behavioural responses. Solid line in a set of models represents relationships present across a set of models. Dashed lines represent relationships expressed in particular syndrome structures. Path 'a' is active in model 2; 'b' in model 3; both 'a' and 'b' are active in model 4. Paths 'c' and 'd' are active in model 5; 'c' and 'e' in model 6; paths 'c'–'e' are all active in model 7. Paths 'd' and 'e' are active in model 8.

concentrated search, for the caches made by the focal subject (Reid & Staddon 1998; Jenkins *in preparation*). Simulated individuals searched randomly, with a preference for moving along the edge of an arena (Jenkins & Breck 1998). Upon finding a cache, the simulated individual searched the immediate area first and resumed random search if no additional caches were found. This index integrated the size, number and spatial dispersion of caches as well as the amount of seeds larder versus scatter hoarded. Individuals who predominantly scatter hoarded seeds and did so in many small and dispersed caches had the highest index scores.

We used two response variables based on these spatial scores in subsequent testing of syndrome structure: the best linear unbiased predictor (BLUP) of an individual's spatial pattern of caching and intra-individual flexibility in spatial pattern of caching. We calculated BLUPs from mixed-model analysis in which the individual was included as a random effect (Kruuk 2004; Reale & Martin *in press*). BLUPs provided an estimate of an individual's 'behavioural profile' (Reale & Martin *in press*) after removing fixed effects (e.g. conspecific cue treatment). We measured intra-individual flexibility using the variance of an individual's rank transformed spatial scores across the four trials ( $I_{\text{var}}$ ). High values of  $I_{\text{var}}$  represented larger within individual variation (greater flexibility in response) while small  $I_{\text{var}}$  values represented less variation (less flexibility). This value was a non-parametric extension to more than two measurements of 'individual consistency' as described by Asendorpf (1990), and is a measure of individual flexibility.

### (iii) Response to a predator stimulus

We determined behavioural responses to predation threat by observing foraging in the presence of a cue of predator presence. Individuals were introduced into a  $0.7 \times 0.7$  m arena and allowed to remain in a nesting chamber and to emerge on their own. As in other tests, various 'natural' structures were located throughout the arena. Sand saturated with 2.5 ml of coyote urine diluted with water to a total volume of 10 ml was used as a simulated predator cue. This sand was located along the centre of the far wall (in relation to the nest chamber), and 10 g of hulled sunflower seeds were placed on top of the saturated sand. *D. merriami* have

previously demonstrated alteration in foraging patterns to similar cues of predation risk, although individual differences in response were not explicitly examined (Herman & Valone 2000). We allowed each individual access to the arena for a period of 10 min during which time behaviours were continuously recorded (Martin & Bateson 1999). After 10 min, we removed the individual from the arena and recorded the mass of seed harvested as a measure of boldness.

### (b) Data analysis

We compared *a priori* hypotheses of syndrome structure using a combination of SEM incorporating latent variables and information-theoretic (I–T) model comparison using AMOS 5.0 (SPSS, Chicago; Shipley 1999; Burnham & Anderson 2002; Johnson 2002). We used four observed variables (described above) to construct structural equation models (SEMs) representing behavioural syndromes (figure 1). Where appropriate we transformed variables prior to SEM analyses (e.g. MIS latency time). Relative explanatory power of the models was compared, penalizing for complexity, using differences in AIC scores (lower scores indicated greater statistical support; Burnham & Anderson 2002; Richards 2005). The SEMs with the lowest AIC scores were considered representative of the syndrome/personality structure of *D. merriami*. Models with AIC scores differing from that of the lowest score by more than two (i.e.  $\Delta\text{AIC} > 2$ ) were considered to be unsupported statistically (Richards 2005).

AIC values were calculated using likelihood discrepancies based on 1000 bootstraps. Bootstrapping was used to calculate likelihood because we assumed multivariate non-normality. To conduct bootstrapping, three missing values (for the amount of seed collected in the presence of a stimulus of predator presence) were replaced with randomly generated values to allow inclusion of data from all individuals. Values were drawn from a normal distribution using the mean and variance from observed trials (model comparison results were concordant across multiple sets of randomly generated values).

### (c) Behavioural syndrome structures

We constructed the following eight models (approx. 10% of all possible models) of hypothesized syndrome structures based on the syndrome literature (figure 2)

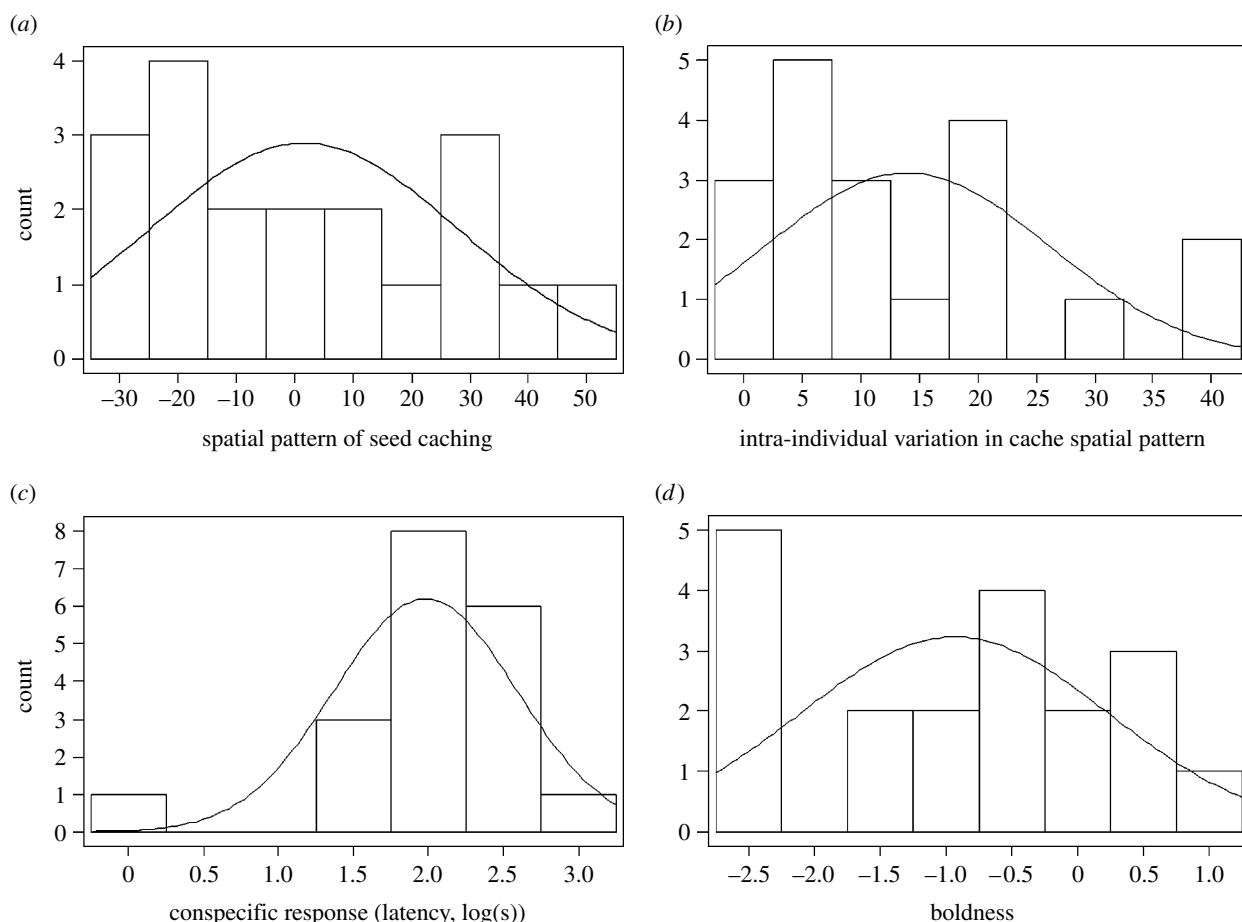


Figure 2. Distributions of behavioural responses. (b) Individual flexibility and (c) conspecific response differed significantly from normal distributions ( $R=0.933$ ,  $p=0.022$  and  $R=0.896$ ,  $p<0.01$ , respectively). (a) Spatial pattern of seed caching and (d) boldness did not differ from normal distributions.

*Model 1.* Behavioural independence, no relationship between behavioural responses. This was the null model for syndrome structure.

*Model 2.* Spatial pattern of seed caching and caching flexibility linked together (figure 2, only path 'a' activated), independent of boldness and conspecific response. Functional context responses may be expected to covary (domain-specific syndrome; Sih *et al.* 2004b).

*Model 3.* Boldness and conspecific response linked (figure 2, only path 'b' activated). This represented a commonly described syndrome structures (Koolhaas *et al.* 1997, 1999; Wilson 1998; Sih *et al.* 2004a,b).

*Model 4.* A two-functional context syndrome containing a caching context syndrome, including flexibility, that varied independently of a boldness and conspecific response syndrome (figure 2, paths 'a' and 'b' activated).

*Model 5.* Food hoarding behaviour and flexibility linked with conspecific response (figure 2, paths 'c' and 'd' activated), forming a domain-general syndrome (Sih *et al.* 2004b).

*Model 6.* Food hoarding behaviour and flexibility linked with boldness (figure 2, paths 'c' and 'e' activated), forming a domain-general syndrome (Sih *et al.* 2004b).

*Model 7.* Full domain-general syndrome (Sih *et al.* 2004b) linking food hoarding and flexibility with boldness and conspecific response (figure 2, paths 'c'–'e' activated).

*Model 8.* Domain-general syndrome of food hoarding behaviour, boldness and aggression with intra-individual flexibility varying independently (figure 2, paths 'd' and 'e' activated).

### 3. RESULTS

All behavioural measures differed considerably between individuals (figure 2). Data differed from normal distributions according to Ryan–Joiner tests (Filliben 1975) for individual flexibility in cache spatial structure ( $R=0.933$ ,  $p=0.022$ ; figure 2b) and, despite transformation, an individual's conspecific response (log-transformed latency time,  $R=0.896$ ,  $p<0.01$ ; figure 2c). Distributions of boldness (seed gathering in the presence of a predator cue) and the spatial pattern of seed caching did not differ significantly from normal ( $R=0.989$ ,  $p>0.1$  and  $R=0.9641$ ,  $p>0.1$ , respectively). The shape of behavioural response distributions also varied considerably (figure 2). While an individual's conspecific response appeared generally unimodal (figure 2c), other behaviours appeared to be more unevenly distributed, with boldness possibly bimodal (figure 2d).

Spearman correlations between behavioural responses ranged from small to medium strengths (table 1; Cohen 1992). Since we utilized an I-T approach to compare models of syndrome structure, correlation probability values are not explicitly considered (Anderson *et al.* 2001). The strongest correlation ( $\rho = -0.282$ ) was between the amount of seed gathered while in the presence of a predator cue (boldness) and conspecific response (mirror image latency; table 1). The direction of the relationship indicated that individuals who collected more seed while in the presence of a predator cue also had shorter latency after first viewing a mirror image. In other words, bolder individuals resumed activity



Table 1. Spearman correlation coefficients for behavioural responses with uncorrected *p*-values in parentheses. (Values in bold along the diagonal are response variable means with standard deviations in parentheses.)

	spatial pattern of seed caching	intra-individual variation in spatial pattern of seed caching	boldness (seed taken; log(g))	conspecific response (latency, log(s))
spatial pattern of seed caching	<b>1.580 (26.136)</b>			
intra-individual variation in spatial pattern of seed caching	0.016 (0.949)	<b>13.965 (12.151)</b>		
boldness (seed taken; log(g))	0.196 (0.420)	0.077 (0.754)	<b>−0.933 (1.172)</b>	
conspecific response (latency, log(s))	0.196 (0.422)	−0.150 (0.539)	−0.282 (0.243)	<b>1.980 (0.611)</b>

Table 2. Results of model comparison using Akaike information criterion (AIC) model comparison results for the eight candidate models. *K* is the number of parameters estimated in a model. Model discrepancy is the bootstrapped (*n* = 1000) maximum-likelihood discrepancy between the model and the data. Smaller AIC values suggest a better fit of the model to data while also penalizing for complexity (*k*). Models whose AIC values differ from that of the top model ( $\Delta$ AIC) by more than 2 are considered to lack explanatory power relative to the top model. Model likelihoods represent the relative likelihood of a model (e.g. model 7 is 1.33 more likely, given the data, than model 5 (1/0.75)).

model	<i>k</i>	model discrepancy	AIC	$\Delta$ AIC	model likelihood
full domain-general syndrome (model 7)	8	3.77	19.77	0.00	1.00
caching behaviour linked with conspecific response (model 5)	7	6.36	20.36	0.59	0.75
bold-aggressive syndrome (model 3)	5	11.59	21.59	1.82	0.40
behavioural independence (model 1)	4	14.03	22.03	2.26	0.32
domain-general syndrome with intra-individual flexibility independent (model 8)	7	8.53	22.53	2.78	0.25
independent syndromes (model 4)	6	11.04	23.04	3.26	0.20
domain-specific caching syndrome (model 2)	5	13.47	23.47	3.70	0.16
caching behaviours linked with boldness (model 6)	7	11.65	25.65	5.88	0.05

more quickly after the perceived appearance of a conspecific. Correlation coefficients ( $\rho = 0.196$  for both; table 1) also suggested that boldness and conspecific response were connected with the spatial pattern of seed caches (table 1). Bolder individuals had a more dispersed cache spatial pattern, as did individuals with longer latencies (table 1). Finally, individuals with lower conspecific response scores (i.e. more aggressive individuals) exhibited less intra-individual variation in caching spatial pattern ( $\rho = -0.150$ ; table 1).

#### (a) Structural equation model comparison

We compared eight different models of behavioural syndromes (figure 1). These models differed in complexity (table 2, '*K*' was the number of parameters estimated) and in whether they incorporated cross-contextual/cross-functional relationships. Despite relatively small correlations, the domain-general syndrome (model 7; figure 1) had the lowest AIC score and best explained the observed data (table 2). This model also statistically differed from the null model of behavioural independence (model 1; figure 1) according to a drop-in-deviance test (deviance<sub>df4</sub> = 10.26,  $p = 0.036$ ).

Two additional syndrome structures required consideration due to  $\Delta$ AIC values less than 2 (models 5 and 3; table 2 and figure 2). Both structures incorporated domain-general relationships between aggression and either caching responses or boldness (figure 2). While the three top models cannot be conclusively distinguished from one another, jointly they provide strong support for the presence of a domain-general syndrome in *D. merriami*.

#### 4. DISCUSSION

Using the novel and generalizable approach of combining SEM and I-T model comparison, we demonstrated that *D. merriami* exhibits a domain-general syndrome incorporating behaviours related to food provisioning, conspecific interaction, predation and flexibility (table 2). The pattern of correlations between behaviours within this syndrome was generally consistent with previous research. As in other rodents (Koolhaas *et al.* 1997, 1999), this syndrome connected boldness to response towards conspecifics. Bolder individuals exhibited lower latency to respond to their mirror image, suggesting that bolder individuals were more aggressive and potentially socially dominant. The negative relationship between aggression and flexibility is also consistent with other reports that aggressive and bold individuals exhibited less flexibility and ability to respond to changing environmental conditions (Koolhaas *et al.* 1997, 1999). The model comparison results and associated correlation coefficients also suggested that connections between boldness and flexibility may have been mediated through conspecific aggression. Further, the model comparison results (table 2) support arguments that behaviours from different functional contexts covary and are constrained in their plasticity by their connections to other behaviours and that domain-general syndromes may be common among organisms (Sih *et al.* 2004a,b; Bell 2007).

Our results also suggest that the combination of I-T and SEM is a more powerful approach to testing behavioural syndrome hypotheses than is the use of bivariate correlation coefficients. Our approach detected

an underlying covariance pattern which would not be interpretable using probability values (table 2 versus table 1). The SEM approach also avoided concerns regarding type I error inflation, an issue in syndrome research (Bell 2007), by considering a restricted subset of *a priori* models (Anderson & Burnham 2002).

Given that *D. merriami* exhibited a domain-general behavioural syndrome, it is likely that the correlated nature of behaviours affects *D. merriami* survival and reproductive success, and results in fitness trade-offs between behavioural responses for the species (Sih *et al.* 2004a,b). For example, response towards predator cues probably directly impacts survival of *D. merriami* and indeed the species has been observed to avoid preferred areas where predators are perceived to have been present (Herman & Valone 2000). Similarly, food hoarding has been considered an important adaptation for *D. merriami* (and other heteromyids) as it allows individuals to survive through periods of low food availability (Jenkins *et al.* 1995; Jenkins & Breck 1998). Levels of aggression towards conspecifics are likely to affect reproductive success by increasing or decreasing reproductive opportunities (Randall *et al.* 2002). How these different selective pressures interact remains unclear for *D. merriami*. Nonetheless, these results suggest that the ability of *D. merriami* populations to respond to selection may be limited by underlying connections between behaviours. Future research should attempt to incorporate multivariate measures of selection, with particular attention being paid to correlative selection (Lande & Arnold 1983; Brodie *et al.* 1995).

The general prevalence of syndromes underlying behaviours affecting fitness has been questioned by some researchers (e.g. Neff & Sherman 2004). However, our results support arguments that behavioural responses may be linked in numerous diverse taxa (Sih *et al.* 2004a,b; Bell 2007).

Since research on behavioural syndromes is still fairly new, theoretical justification for the maintenance of syndromes as well as the causal mechanisms responsible for syndrome structures remain to be resolved (Bell 2007). However, some researchers have proposed that temporal or spatial heterogeneity may lead to the maintenance of syndrome structures with different combined strategies being most effective under particular conditions (Dingemanse *et al.* 2004). Alternatively, multiple fitness peaks in a multivariate landscape may lead to the maintenance of syndrome structures and equivalent fitnesses for different strategies. It is not clear at this point what factors have led to the maintenance of syndrome structure in *D. merriami*. However, owing to the species' expansive range as well as the spatial and temporal stochasticity inherent in the arid ecosystems it inhabits, *D. merriami* may prove to be an ideal species with which to test proposed mechanisms of syndrome maintenance.

This research was conducted according to the guidelines for the use of animals published by the Animal Behaviour Society and was carried out in accordance with the legal requirements of the United States of America and the University of Nevada, Reno (IACUC Protocol no. A04/05-04).

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